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14. ABSTRACT In this project, we measured muscle activity, body movements, and flow patterns during linear acceleration in the bluegill sunfish, <i>Lepomis macrochirus</i> . Animals with flexible bodies, like fishes, face a tradeoff for rapid movements. To produce high forces, they must make high amplitude movements of their fins, tails, or other propulsors, which requires that the propulsors be flexible to bend to high amplitude. However, the reaction forces from the environment are then large, which requires that the propulsors be stiff to resist these forces. Indeed, when we measured wake flow patterns, we found that the momentum flux was higher during acceleration, corresponding					
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Report Title

Final Report: Neuromuscular Control of Rapid Linear Accelerations in Fish

ABSTRACT

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Enter List of papers submitted or published that acknowledge ARO support from the start of the project to the date of this printing. List the papers, including journal references, in the following categories:

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(b) Papers published in non-peer-reviewed journals (N/A for none)

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Paper

TOTAL:

Number of Papers published in non peer-reviewed journals:

(c) Presentations

Boden, A. L., Wise, T. N., Schwalbe, M. A. B. and Tytell, E. D. (2015). Co-contraction of red muscle during acceleration in bluegill sunfish (*Lepomis macrochirus*). Presented at the Society for Integrative and Comparative Biology, West Palm Beach, FL (no. P3-136), Jan. 6, 2015.

Schwalbe, M. A. B., Boden, A. L., Wise, T. N. and Tytell, E. D. (2015). Neuromuscular control of rapid linear accelerations in the bluegill sunfish. Presented at the Society for Integrative and Comparative Biology, West Palm Beach, FL (no. 4.2), Jan. 4, 2015.

Wise, T. N., Boden, A. L., Schwalbe, M. A. B. and Tytell, E. D. (2014). Hydrodynamics of linear accelerations in *Lepomis macrochirus*. Presented at the Society for Integrative and Comparative Biology, Division of Vertebrate Morphology regional meeting, New Bedford, MA, Nov. 1, 2014.

Number of Presentations: 3.00

Non Peer-Reviewed Conference Proceeding publications (other than abstracts):

<u>Received</u>	<u>Paper</u>
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Number of Non Peer-Reviewed Conference Proceeding publications (other than abstracts):

Peer-Reviewed Conference Proceeding publications (other than abstracts):

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(d) Manuscripts

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Number of Manuscripts:

Books

Received Book

TOTAL:

Received Book Chapter

TOTAL:

Patents Submitted

Patents Awarded

Awards

Graduate Students

<u>NAME</u>	<u>PERCENT_SUPPORTED</u>
FTE Equivalent:	
Total Number:	

Names of Post Doctorates

<u>NAME</u>	<u>PERCENT_SUPPORTED</u>
Margot Schwalbe	0.25
Vishesh Vikas	0.55
FTE Equivalent:	0.80
Total Number:	2

Names of Faculty Supported

<u>NAME</u>	<u>PERCENT SUPPORTED</u>	National Academy Member
Eric Tytell	0.00	
FTE Equivalent:	0.00	
Total Number:	1	

Names of Under Graduate students supported

<u>NAME</u>	<u>PERCENT SUPPORTED</u>	Discipline
Alexandra Boden	0.20	Biosciences
Tyler Wise	0.08	Biosciences
FTE Equivalent:	0.28	
Total Number:	2	

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NAME

Total Number:

Names of personnel receiving PHDs

NAME

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Sub Contractors (DD882)

Inventions (DD882)

Scientific Progress

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See attachment.

Neuromuscular control of rapid linear accelerations in fish: Final Report

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Abstract

In this project, we measured muscle activity, body movements, and flow patterns during linear acceleration in the bluegill sunfish, *Lepomis macrochirus*. Animals with flexible bodies, like fishes, face a tradeoff for rapid movements. To produce high forces, they must make high amplitude movements of their fins, tails, or other propulsors, which requires that the propulsors be flexible to bend to high amplitude. However, the reaction forces from the environment are then large, which requires that the propulsors be stiff to resist these forces. Indeed, when we measured wake flow patterns, we found that the momentum flux was higher during acceleration, corresponding to high forces. Bluegill use their muscles to both produce power for rapid movements, but also to appear to use them to stiffen their bodies. During acceleration, but not during steady swimming, muscle tends to become active as it is being stretched, and muscle on the left and right side of the body are active simultaneously; both of these effects should increase body stiffness. These results suggest that fish, and perhaps other soft-bodied organisms, can actively modulate the effective stiffness of their bodies in order to accelerate rapidly while also being able to swim efficiently.

To stay alive, most animals must do many different behaviors with different energetic and mechanical requirements. They travel long distances efficiently to find food or mates, but they also accelerate rapidly to catch prey or escape predators. Computational results suggest that for efficient long-distance travel, an animal might require a compliant body, able to store and release elastic energy efficiently (Tytell et al., 2010). For rapid acceleration, one needs the opposite: a stiff and strong body, able to transmit large forces from the muscles to the environment (Tytell et al., 2010). How do animals balance these conflicting demands?

Moreover, acceleration itself has conflicting demands. To accelerate, animals often move their tails, fins, or other propulsors with high amplitudes (Tytell, 2004), which requires them to be flexible. However, reaction forces from the environment are then large, which requires that the propulsors be stiff to effectively resist these forces.

Muscle is a versatile actuator that can potentially meet these conflicting demands. It can produce power, absorb energy, or modulate effective stiffness (Long, 1998; McMahon, 1984; Weiss et al., 1988). In particular, muscles are stiffer when they are activated by the nervous system than when they are passive (Weiss et al., 1988), and they are even stiffer when active during lengthening (called an “eccentric” contraction) (Long, 1998). During reaching movements, humans and other

animals increase the effective stiffness of their arm joints by contracting muscles on either side of the joint; the additional stiffness helps to stabilize against unpredictable perturbations and increase final accuracy (Burdet et al., 2001; Gribble et al., 2003).

The goal of this project was to examine whether the bluegill sunfish, *Lepomis macrochirus*, use co-contraction or eccentric contractions during accelerations, and how the muscle activation changes during different strengths of accelerations. To make these measurements, we also developed a small inertial measurement unit (IMU) that could accurately measure body orientation and dynamic acceleration. The primary results of the work were

- We developed and tested several techniques for estimating body orientation and dynamic acceleration from noisy IMU data. We developed an approach using an extended Rauch-Tung-Striebel smoother (ERTSS), a smoothing algorithm similar to the extended Kalman filter (Särkkä, 2013). While ERTSS smoother accounts for gyro drift and dynamic acceleration in a coherent way, further work will be required to fully constrain the filter. A simpler approach, based on Madgwick et al. (2011), which minimizes the difference between gyro- and accelerometer-based orientation estimates, gives a good estimate of both orientation and dynamic acceleration.
- Bluegill sunfish use both co-contraction and eccentric contractions during acceleration, presumably increasing the effective stiffness of the body. Co-contraction is strongest when accelerations start from a low swimming speed; if fish are already swimming fast, co-contraction is less pronounced. Similarly, fish seem to use more eccentric contractions when they start accelerating from low speed.
- Initial analyses show that fish also modulate the strength of the acceleration by changing both co-contraction and eccentric contractions. We hypothesized that these effects would be most pronounced at the tail, because that is where the fluid forces are highest. Instead, we saw the largest changes in activation in the midbody region, and much smaller effects close to the tail.
- We measured flow around bluegill as they accelerated. Momentum flux (force), based on the wake, increases substantially. Unlike accelerating eels (Tytell, 2004), initial analysis shows that the wake does not change structure in a qualitative way.

These findings suggest several avenues to continue and extend this work:

- We are developing an open source toolbox, based on an Arduino microcontroller, to run the IMU and estimate orientation and dynamic acceleration. We are continuing work on the filters and the analysis toolbox and intend to submit a publication in the fall.
- In the proposal, we planned to perturb the fish during acceleration, to investigate how acceleration is controlled and to examine the relative balance between planned feedforward motor commands and reflexive feedback modulation. Our proposal was to train fish to accelerate toward a wand to receive food. Unfortunately, fish did not feed consistently when electrodes were implanted.

These tests are likely to reveal important aspects of how rapid movements are controlled, but will have to be done using a negative stimulus such as a object accelerating toward the fish. If the object changes its trajectory as the fish begins to accelerate, we can investigate how rapidly and at what times during the behavior the fish can alter it.

- We have documented that fish change their muscle activation during acceleration in ways that probably increase effective body stiffness, but we have not actually measured the change in

stiffness. In a different project, W911NF-14-1-0268, “Coupling mechanical and neural properties for effective and adaptable locomotion”, we are developing an apparatus to measure passive and active body stiffness in lampreys. If we extend this apparatus to work on bluegill sunfish or other fishes, we will be able to directly measure the change in body stiffness, based on the changes we observed in muscle activity.

- Fish seem to use both co-contraction and eccentric contractions during acceleration differently at different locations along the body. What are the performance consequences of the two types of activity? With co-contraction, muscles on opposite sides are opposing each other, while in eccentric contractions, muscles may be opposing fluid forces; co-contraction may therefore require more energy. The differences could be tested using a computational model (e.g. Tytell et al., 2010) or robotic models (e.g. Wen and Lauder, 2013).

1 Primary findings

1.1 Measurement of dynamic acceleration from IMUs

Inertial measurement units (IMUs) with gyroscopes and accelerometers have been used in many situations to measure orientation (e.g. Luinge and Veltink, 2005; Madgwick et al., 2011; Noda et al., 2014), but these approaches often assume that dynamic acceleration is zero. The gyro measures angular velocity, but has noise and a slowly drifting bias. The accelerometer measures total acceleration, which is the sum of gravitational acceleration and dynamic acceleration. Two primary classes of algorithms have been used before: complementary filters and Kalman filters.

For a complementary filter, one can (in essence) integrate the gyro signal to estimate orientation and combine that with the accelerometer’s estimate of the direction of the gravity vector. Note that one cannot directly integrate the angular velocities in 3D, because the velocities are defined relative to the sensor’s moving coordinate system. Following Madgwick et al. (2011), we estimated the quaternion orientation of the earth frame relative to the sensor $\hat{\mathbf{q}}_{est,t}$. We use a bandpass filter to eliminate bias and noise, then update the estimate based on the angular velocities:

$$\hat{\mathbf{q}}_{\omega,t} = \hat{\mathbf{q}}_{est,t-1} + \frac{1}{2} \hat{\mathbf{q}}_{est,t} \otimes \omega_t \quad (1)$$

where $\hat{\mathbf{q}}_{est,t}$ is the current estimate of the orientation of the earth frame relative to the sensor, \otimes is a quaternion product, and $\omega_t = [0 \ \omega_x \ \omega_y \ \omega_z]$. Similarly, the accelerometer can be used directly to estimate a quaternion orientation $\hat{\mathbf{q}}_{a,t} = [0 \ a_x \ a_y \ a_z]$, where a_x , a_y , and a_z are the accelerometer readings. If there is no dynamic acceleration or noise, $\hat{\mathbf{q}}_{a,t}$ is exactly correct. The procedure developed by Madgwick et al. (2011) then takes one gradient descent step to minimize the difference between $\hat{\mathbf{q}}_{a,t}$ and $\hat{\mathbf{q}}_{\omega,t}$, where the size of the step is related to the magnitude of the angular velocities. When angular velocity is low, then the accelerometer readings are a good estimate of the true orientation, and so the step is small, keeping the estimate close to the accelerometer value; when angular velocity is high, the step is large, moving close to the estimate from integrating the gyro.

The complementary filter, though, does not explicitly include dynamic acceleration. To account for that more directly, and to account for drift in the gyro, we developed an extended Kalman filter based smoothing algorithm (extended Rauch-Tung-Striebel smoother, or ERTSS; Särkkä, 2013). We estimated a state \mathbf{x} of the sensor that includes both the gyro bias and dynamic acceleration: $\mathbf{x} = [\Theta \ \mathbf{b} \ \mathbf{a}_{dyn}]^T$, where Θ is the orientation of the sensor, \mathbf{b} is the bias of the gyro, which drifts

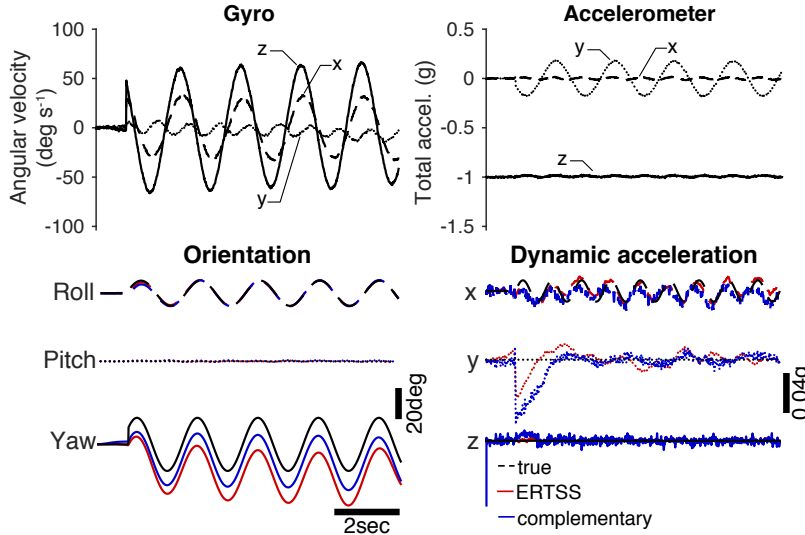


Figure 1: Comparison of the two filters for processing IMU data and estimating dynamic acceleration. The top two panels show a simulated IMU recording with realistic levels of noise. We simulated a tail beat that includes yawing and rolling at the tail beat frequency, which leads to a pulse of forward acceleration at twice the tail beat frequency. The bottom panels show the performance of the two filters. The ERTSS filter is shown in red; the complementary filter is shown in blue; and the true values are shown in black.

according to a slow random walk, and \mathbf{a}_{dyn} is the dynamic acceleration, which is also modeled as a random walk with a coefficient c_a . The c_a coefficient defines the frequency band in which we expect dynamic accelerations, and must currently be tuned manually for each situation.

Fig. 1 shows the performance of the two filters on simulated data that approximates a fish beating its tail from side to side, rolling with the tail beat, and accelerating slightly forward twice per tail beat. Both filters perform fairly well, but the ERTSS filter tends to diverge, particularly on the yaw estimate. In general, yaw is not possible to estimate uniquely, because we only have the gravity vector as a reference. We cannot correct for noise on the yaw axis. The ERTSS filter allows us to provide periodic corrections to the yaw angle, based on the video. However, its estimates are currently quite sensitive to the c_a parameter and the covariance matrices. If the parameters are set incorrectly, the estimates can diverge. Because of this instability, we are currently using the complementary filter, but we intend to continue developing the ERTSS filter. When the IMU is immersed in water, the drift tends to be quite small; if drift is larger, though, the complementary filter would likely perform much worse, and the ERTSS filter would be more appropriate.

1.2 Kinematics, muscle activity, and flow patterns during acceleration

We gathered a large amount of data during the nine months of this project: steady swimming and acceleration behaviors from five fishes with high speed video, IMUs, and electromyography electrodes, and the behaviors from three fish with high speed video, IMUs, and particle image velocimetry. Data analysis is ongoing and will continue using funding from Tufts University or other sources. Below, we report on initial analyses of one individual.

Flow patterns We measured flow around the fish and in its wake using particle image velocimetry (Tytell, 2011). Fine copper wires were soldered to an InvenSense MPU-9250 digital IMU, which was then encased in epoxy. The IMU was sutured to the fish, just anterior to the dorsal fin. During steady swimming, the fish produces a standard reverse von Karman wake, which has

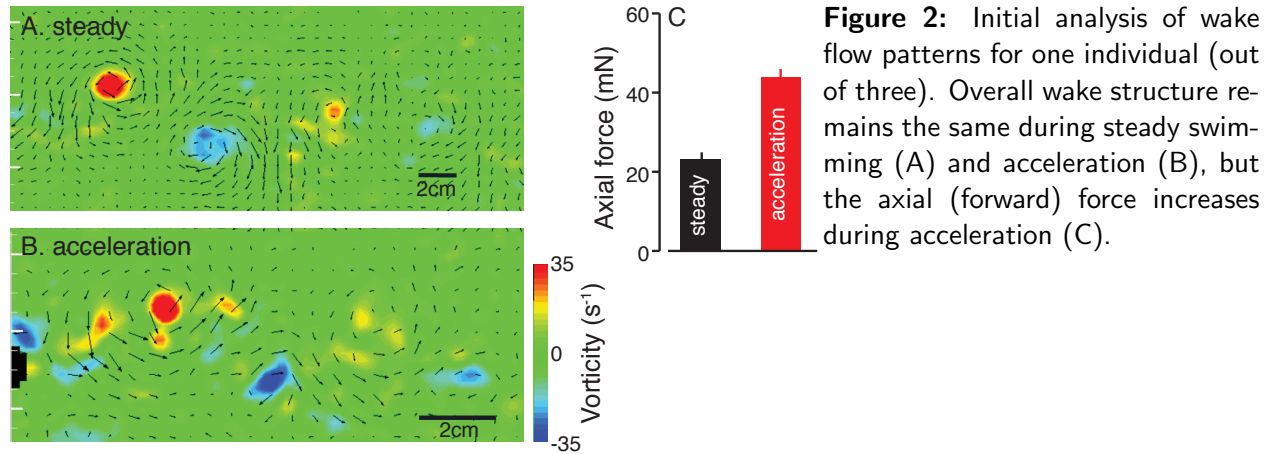


Figure 2: Initial analysis of wake flow patterns for one individual (out of three). Overall wake structure remains the same during steady swimming (A) and acceleration (B), but the axial (forward) force increases during acceleration (C).

two single vortices (2S) shed per tail beat (Fig. 2A), as has previously been observed (Drucker and Lauder, 2001; Tytell, 2007). When the fish begins to accelerate, the wake does not change qualitatively in structure, but the flows become stronger (Fig. 2B). This is different from the pattern observed for accelerating eels, in which the wake changes from two pairs of vortices (2P) to a 2S structure during acceleration (Tytell, 2004). By measuring the circulation Γ of vortices in the wake, we can estimate the mean force (Tytell, 2011)

$$F_{mean} = \frac{\pi \rho \Gamma d h}{4T} \cos(\alpha) \quad (2)$$

where ρ is the density of water, d is the distance between a vortex pair, h is the height of the fish's tail, T is the tail beat period, and α is the angle of the vortex pairs to the swimming direction. As expected, mean forces are higher during acceleration than during steady swimming (Fig. 2C).

Kinematics and muscle activity As above, an IMU was sutured to the fish, just anterior to the dorsal fin. Fine wire EMG electrodes were implanted in red muscle, which powers steady swimming and low to moderate accelerations, at three or four positions along both sides of the body (6 or 8 electrodes total). Fish were filmed at high speed from below while swimming against a flow at a range of different steady swimming speeds. Accelerations were elicited by startling the fish from behind, either by moving a rod toward it, or by clicking forceps. Fig. 3 shows kinematics and muscle activation patterns for accelerations and steady swimming starting from a relatively high swimming speed of $1.75Ls^{-1}$. Each point represents a mean over half a tail beat (when the tail moves across to the left or the right); over that half tail beat, we also identified the peak forward acceleration. Side-to-side amplitude of the head and the tail (Fig. 3A) both increased as acceleration increased. Tail beat frequency also increased (Fig. 3B).

Muscle at different positions along the body changed activity differently as accelerations became stronger. Muscle in the midbody, just posterior to the pectoral fin, tended to become active for a longer fraction of the cycle (blue points, Fig. 3C). Duty cycle approached or exceeded 0.5, which indicates co-contraction, particularly at the highest acceleration. Muscle close to the tail, in the caudal peduncle, began with a relatively high duty cycle, which decreased as accelerations became stronger (red points, Fig. 3C). Midbody muscle became active earlier relative to curvature as accelerations became stronger (blue points, Fig. 3D). Negative onset phase indicates that muscle

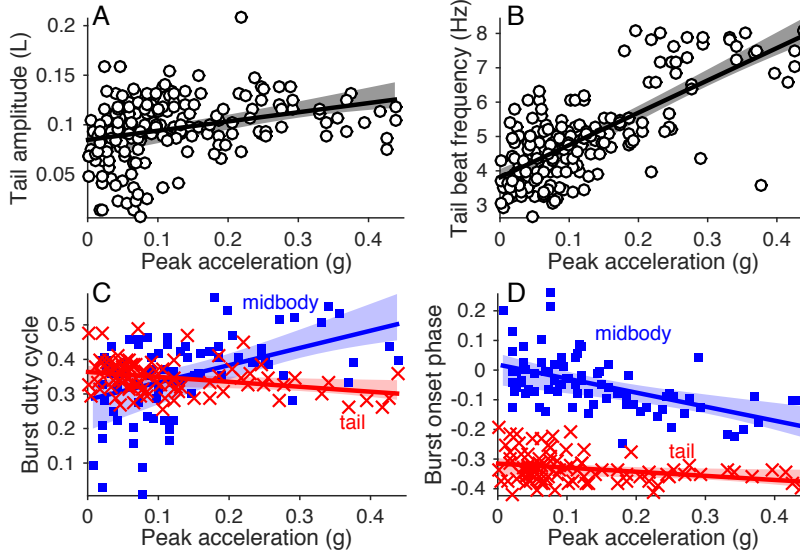


Figure 3: Summary of initial analysis of acceleration kinematics and muscle activity for one individual fish (out of five). Tail amplitude (A) and frequency (B) increase as acceleration increases. Muscle activity changes differently at different locations along the body. Duty cycle (C; the fraction of the period in which the muscle is active) increases with higher acceleration for midbody segments (blue), but decreases for tail segments (red). For both locations, muscles become active earlier relative to curvature (D) as acceleration increases, but the effect is more pronounced for the midbody.

turns on as it is being lengthened, which is called an eccentric contraction and produces negative work. Muscle near the tail were active even earlier in the cycle, producing almost entirely negative work, but it also activated earlier for strong accelerations (red points, Fig. 3D).

This pattern of differences in muscle activity along the body is the opposite of what we hypothesized. We hypothesized that muscle near the tail would need to be stiffer during accelerations, because fluid forces are high there. We did observe high fluid forces (Fig. 2C), but in fact it appears that most of the change in effective body stiffness may be happening at the midbody. Further analysis will be needed to understand how fish partition the power generating and body stiffening roles of muscle along the body and over time.

2 Future directions

Work on this project is continuing, with support from Tufts University and other sources. In particular, we are still analyzing the data. We plan to consider how muscle activation differs over time, during the course of an acceleration behavior, and also to examine how the activity changes over the body. We will also continue analysis of the fluid dynamic data to estimate forces at different points along the body. Ongoing work will estimate temporally and spatially resolved forces by estimating fluid pressure (Dabiri et al., 2014). By comparing force at a particular point along the body and curvature there, we may be able to approximate effective stiffness. We plan to submit a paper on the kinematics and muscle activity in the fall, and a second paper on the fluid dynamics in the winter or early next year.

We are also continuing work on the development of IMUs for use on small animals. We are developing and testing a toolbox, using an Arduino microcontroller to control the IMU and Matlab to sample, record, and process the data. Further work on the ERTSS filter will identify a systematic way of choosing the parameters and the covariance matrices. We plan to submit a paper on the technique in the fall.

2.1 Identifying feedback and feedforward control during acceleration

One goal of the project was to identify feedback and feedforward control components of acceleration in fishes. Fish learn quickly to feed from a wand, and will accelerate toward it, if it is visible. We planned to perturb acceleration by moving the wand after the fish began accelerating. Unfortunately, we found that fish will not feed consistently when they have EMG electrodes in their muscles. This portion of the project is still feasible, but will require using aversive stimuli, such as an object moving toward the fish, or a looming visual stimulus. As we originally proposed, we will perturb the acceleration by altering the stimulus after the acceleration began. For example, we could alter the trajectory of the moving object. As before, we can add noise to the system by introducing turbulent eddies, which will help to separate feedforward, pre-set patterns from feedback modulated patterns.

To perturb the behavior in a consistent way, however, will require tracking the fish's location and orientation in real time, and then modulating the stimulus based on the fish's response. We are currently discussing how to proceed on this project idea with Noah Cowan and his group.

2.2 Measuring active and passive body stiffness

We now have good evidence that fish modulate muscle activity during rapid movements in a way that suggests that they are actively changing their effective body stiffness. To directly measure the change in body stiffness, we are constructing a device to bend the body of a lamprey, stimulate its muscles, and measure the forces involved (after Long, 1998; Long and Nipper, 1996). That work is currently funded under W911NF-14-1-0268, "Coupling mechanical and neural properties for effective and adaptable locomotion". Relatively small changes to the apparatus should let us use it for bluegill sunfish. Then, we could approximate the activation changes we observed during swimming and measure how the stiffness changes.

2.3 Differences between co-contraction and eccentric contractions

We have observed that fish use both co-contraction and eccentric contractions during acceleration, and that they use them differently at different locations along the body (Fig. 3). An important difference between the two types of contractions is that co-contraction, by definition, means that one muscle is resisting the action of another muscle. Since the muscles are fighting one another, they probably require extra metabolic energy. In contrast, an eccentric contraction may occur when a muscle resists the force from the environment. In general, eccentric contractions require very little energy (Ruina et al., 2005). Thus, there may be very different energetic consequences to the use of different types of contractions. Are there other performance consequences? To answer this question, we could use a computational model (after Tytell et al., 2010) or robotic models (after Wen and Lauder, 2013).

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